Technical Report No. 60

OXYGEN CONSUMPTION, EVAPORATIVE WATER LOSS AND BODY TEMPERATURE IN THE SOOTY TERN, *STERNA FUSCATA*

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PREFACE

The Sooty Tern is said to be the most abundant sea bird in the world. We believe that this tern has nested on Manana Island (an offshore island at the SE tip of Oahu) in modern times only since 1947, but the breeding population now numbers about 100,000 birds.

All birds must be physiologically and/or behaviorally adapted to their environment, whether it be a volcanic tropical island or a rain forest. We think it of interest, therefore, to compare the data presented in this report with that given for rain forest species in Technical Report No. 9.

Andrew J. Berger

ABSTRACT

1. The oxygen consumption, total evaporative water loss, and deep-body temperature of Sooty Terns were measured at air temperatures within the range 10-45°C.

2. At air temperatures from 10°C to 30°C, the cloacal temperatures were relatively constant, the temperature of the fledglings tending to exceed that of the adults. At air temperatures of 35°C and higher, the birds became hyperthermic.

3. The thennoneutral temperature was approximately 30°C. The heat production of the terns was lower than the predicted value for non-passerine birds of their weight.

4. Thermal polynea was observed at the higher air temperatures, but at an air temperature of 44-45°C, only one bird was able to dissipate heat in excess of heat production, by evaporative cooling.

5. The calculated thermal conductance was constant at air temperatures of 10-30°C, but the conductance increased at higher temperatures.

6. It was concluded that Sooty Terns are not especially proficient at evaporative cooling, in spite of the thermal demands of their tropical environment. They appear to rely also on a rather low level of heat production, air movement and behavioral mechanisms of temperature regulation.

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INTRODUCTION

The Sooty Tern (Sterna fuscata) is widely distributed throughout the tropical oceans, and it establishes nesting colonies on many of the islands within its range. The islands are typically of low latitude and low profile, and they are therefore exposed to maximal solar radiation during the day, imposing a potential heat load on ground-nesting birds, such as Sooty Terns. Howell and Bartholomew (1962) conducted a field study of temperature regulation in the Sooty Tern on Midway Island in the Leeward Chain of the Hawaiian Islands. Their study demonstrated the importance of behavior in thermoregulation, but necessarily was only implicit concerning the role of physiological regulation.

We have had an opportunity to investigate some of the physiological aspects of temperature regulation in adult and immature fledgling Sooty Terns from a nesting colony on Manana Island, off the southeastern coast of Oahu, Hawaii. This report deals with the roles of energy metabolism and evaporative water loss in temperature regulation by the Sooty Tern.

MATERIALS AND METHODS

Experimental animals. - The Sooty Terns were collected on the nesting colony at Manana Island. They were maintained for 2 to 4 days in a cage, subject to natural photoperiod, at the Manoa campus of the University of Hawaii or at the University's Kewalo Marine Laboratory in Honolulu. While captive they were fed thawed, fresh-frozen squid or smelt, and they were provided with a shallow pan of sea water for bathing and drinking. With the exception of one bird that perished during the study, all were released following their confinement.

Five adult birds, weighing an average of 155.9 ± SD 16.1 g, were captured and measured in August 1972. One fledgling immature bird was used in August 1972, and two others in August 1973. The average weight of the three fledglings, all capable of flight, was 138.6 ± SD 5.3 g. The average weight of all 8 birds was 149.4 ± SD 15.4 g. Body temperatures were measured, under field conditions, on an additional 42 birds.

Body temperatures. - Field measurements of body temperature were made by netting non-nesting birds resting on the ground in the colony, using a long-handled net. Body temperatures were determined within 30 sec of capture by inserting a vinyl ensheathed small-animal thermistor probe, connected to a Y.S.I. Telethermometer, at least 5 cm into the cloaca.

Laboratory measurements of body temperature were made simultaneously with measurements of oxygen consumption, ambient temperature, and evaporative water loss, by inserting a vinyl ensheathed copper-constantan thermocouple at least 5 cm into the cloaca. The thermocouple was attached to a Speedomax recording potentiometer or to a Bailey amplifying thermometer. After insertion of the thermocouple into the cloaca the leads were attached firmly to the rectrices with surgical clips, to prevent withdrawal of the thermocouple.

Ambient temperature. - Field ambient temperatures were measured with a Y.S.I. Telethermometer using appropriate prcbes. Dry-bulb and wet-bulb temperatures were measured with a sling psychrometer. Black-blub temperature was measured with a mercury thermometer enclosed in a black metal globe.

Laboratory ambient temperatures were monitored with copper-constanstan thermocouples inserted into the respirometer chamber and attached either to the Speedomax recording potentiometer or the Bailey amplifying thermometer.

Oxygen consumption. - Oxygen consumption was measured in an open-airflow system with a Beckman Model E2 paramagnetic oxygen analyser. Air, dried by passage through indicating Drierite or magnesium perchlorate, and flowing at rates between 1,600 and 1,837 ml/min, was metered through a 9.751 respirometer chamber constructed from a wide-mouthed jar. The chamber was equipped with ports for the introduction and removal of air, and for the introduction of thermocouples for measurements of ambient temperature (T_a), and body temperature (T_b); the bird rested on a hardware cloth platform, over mineral oil, which prevented evaporation from any excreta voided.

Each Sooty Tern was weighed immediately before being placed in the respirometer chamber and again upon removal from the chamber. Weights during periods of measurements of oxygen consumption were interpolated. The chamber bearing the bird was then placed in a Hotpack, dimly-illuminated, constant-temperature cabinet equipped with heating and refrigeration units and blowers. Temperature control within the respirometer chamber was ± 0.5°C. At air temperatures of 10, 20, 30, 35 and 40°C the birds were allowed to adjust to each temperature for a period of one hour, following which the oxygen consumption was measured at that temperature for a period of 30 min. For measurements at T_a = 44 to 45°C, the air temperature was increased rapidly after measurements at T_a = 40°C; the bird was allowed a 15 min. period of adjustment to T_a = 44 to 45°C, followed by a 20 min period of measurements. The rate of oxygen consumption was measured at 5-min intervals. For

calculation of standard metabolism, the two lowest measurements recorded for each individual at each T_a, corrected to S.T.P., were used. All measurements were made between 1000 and 1730 hr, and the birds were generally quiescent.

Evaporative water loss. - Evaporative water loss (EWL) was measured simultaneously with measurements of oxygen consumption. In August 1972 EWL was measured gravimetrically, with U-tubes filled with Drierite attached to the airline downstream from the respirometer chamber; a second U-tube measured the amount of water vapor in the dried incurrent air. In August 1973, EWL was measured with a Hygrodynamics Model 15-3001 electric hygrometer with sensing units placed both upstream and downstream from the respirometer chamber. The two methods gave consistently equivalent results.

RESULTS

Body temperatures. - Body temperatures of Sooty Terns taken on the nesting colony at Manana Island on 24 August 1972, and 4 August 1973, are summarized in Table I. The colony was located at an elevation of about 8 m, on open sand, and about 25 m from the water's edge, quite exposed to ocean breezes from the south. On 24 August 1972 there was only a very light breeze, while on 4 August 1973, the breeze was noticeably stronger. Although the black-bulb temperature was lower on the earlier date, the body temperatures of the fledglings were significantly higher ($P < .05$); no adults were measured on the later date, as none could be captured. In addition, the mean body temperature of the four adults on 24 August 1972 ($\bar{x}$, T_b = 41.7°C) was significantly higher ($P < .05$) than that of the 26 fledglings ($\bar{x}$, T_b = 40.6°C) on the same day.

Body temperatures of adult and fledgling Sooty Terns, measured under laboratory conditions with controlled T_a, are indicated in Fig. 1. Between T_a = 10 and 30°C, T_b was fairly constant; that of the fledglings (ca. 40°C) was typically higher than that of the adults (ca. 38.5°C). At T_a = 35°C and higher, T_b increased dramatically, and similarly, for both adults and fledglings. The mean T_b for the 5 adults and 2 fledglings, measured between T_a = 44 and 45°C, was 44.3°C, which did not differ significantly ($P > .05$) from the mean T_a (44.6°C) at which they were measured. The highest T_b measured (46.0°C) was that of an adult at T_a = 44.7°C; this bird died on the night following this exposure.

Oxygen consumption. - The relationship between oxygen consumption and T_a is

TABLE 1. Cloacal temperatures of Sooty Terns in the Nesting Colony on Manana Island, Hawaii.

Date (time)	Air temp. in the shade °C	Substrate temp. °C	Black-bulb temp. °C	Relative Humidity %	Body Temperatures, °C Adults $\bar{x}$ + SD	Adults No.	Fledglings $\bar{x}$ + SD	Fledglings No.
24 Aug. 1972 (1230-1507 hr)	30.9	> 50	42.2	62	41.7 ± 0.1	4	40.6 ± 1.0	26
4 Aug. 1973 (1000-1108 hr)	27-30	36-47	46.4	65	--	--	38.9 ± 0.6	12

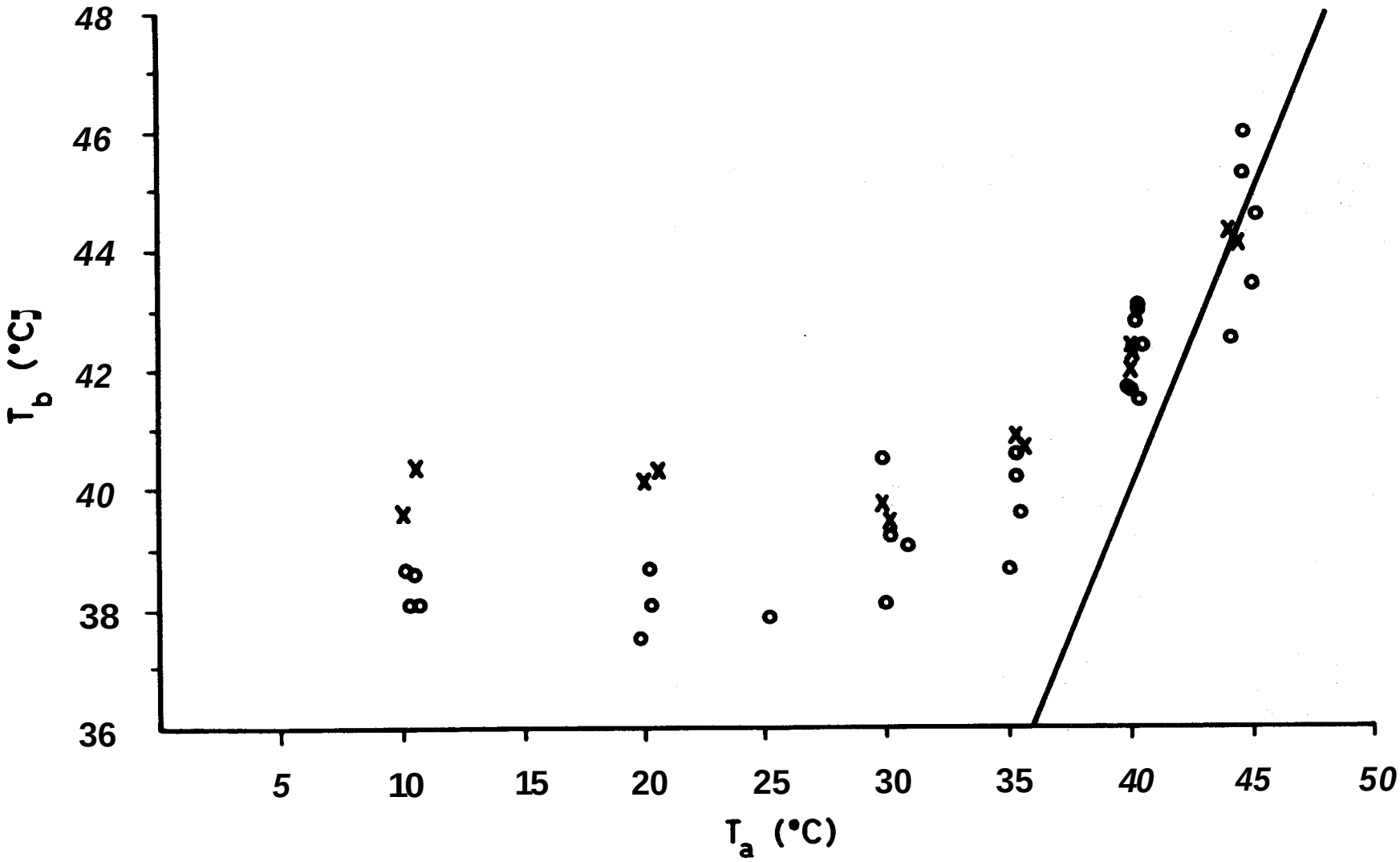

FIG. 1. The relationship between body temperature (Tb) and ambient temperature (T_a) in adult (0) and fledgling (X) Sooty Terns. The diagonal line indicates equality between Tb and Ta.

shown in Fig. 2, which reveals a curvilinear relationship for both adults and fledglings. Below T_a = 30°C, the fledglings appear to have rates of oxygen consumption lower than those of the adults, with the suggestion,of a broader thermal neutral zone. Both adults and fledglings are in thermal neutrality at T_a = 30°C, with the former having a very narrow thermal neutral zone or point, at about that T_a. The standard metabolic rate (SMR) of four adults and two fledglings, measured at T_a = 30 ± 0.5°C, was 0.98 ± SD, 0.11 ml O_2/ghr; the mean weight of the six birds at the time of measurement was 147.5 ± SD, 11.3 g (the SMR of the adults, with a mean weight of 150.4 ± SD, 13.0 g, was 0.97 ± SD, 0.14 ml O_2/ghr; that of the fledglings, weighing 141.7 ± SD, 2.2 g, was 1.02 ± SD, 0.03 ml O_2/ghr). Above T_a = 30°C oxygen consumption increased rapidly, with that of the fledglings appearing to be higher than that of the adults.

Evaporative water loss. - Weight-relative rates of evaporative water loss in relation to T_a are shown in Fig. 3. Both adult and fledgling Sooty Terns have rates of EWL that are directly related to T_a, with only slight increases from T_a = 10 to 35°C; above T_a = 35°C, the increase in EWL is very marked. Between T_a = 10 and 40°C the rate of EWL of fledglings generally exceeds that of the adults.

Expressed as a function of oxygen consumption, EWL is also directly related to T_a (Fig. 4). Again, at the lower temperatures (T_a = 10-35°C), the EWL of fledglings exceeds that of adults, but at the higher temperatures (T_a = 40-45°C) there appear to be no differences between the two age groups. When the EWL values are converted into the relationship between heat produced by metabolism (M) and heat dissipated by evaporation (E), E is generally less than M, even at the highest ambient temperatures. Only one individual Sooty Tern (an adult) was able to dissipate, by evaporative cooling, more heat than was being produced by metabolism, at a T_a of 44-45°C.

DISCUSSION

Simultaneous measurements of oxygen consumption, body temperature, and evaporative water loss afford values for the calculation of dry thermal conductance (C), according to the equation $C = (M-E)/T_b - T_a$, where M and E represent weight-specific heat production and heat dissipation, respectively (after Dawson and Bennett, 1973). In making these calculations it was assumed that consumption of 1 ml O_2 yields 4.8 cal, and evaporation of 1 mg H_2O dissipates 0.58 cal. Dry

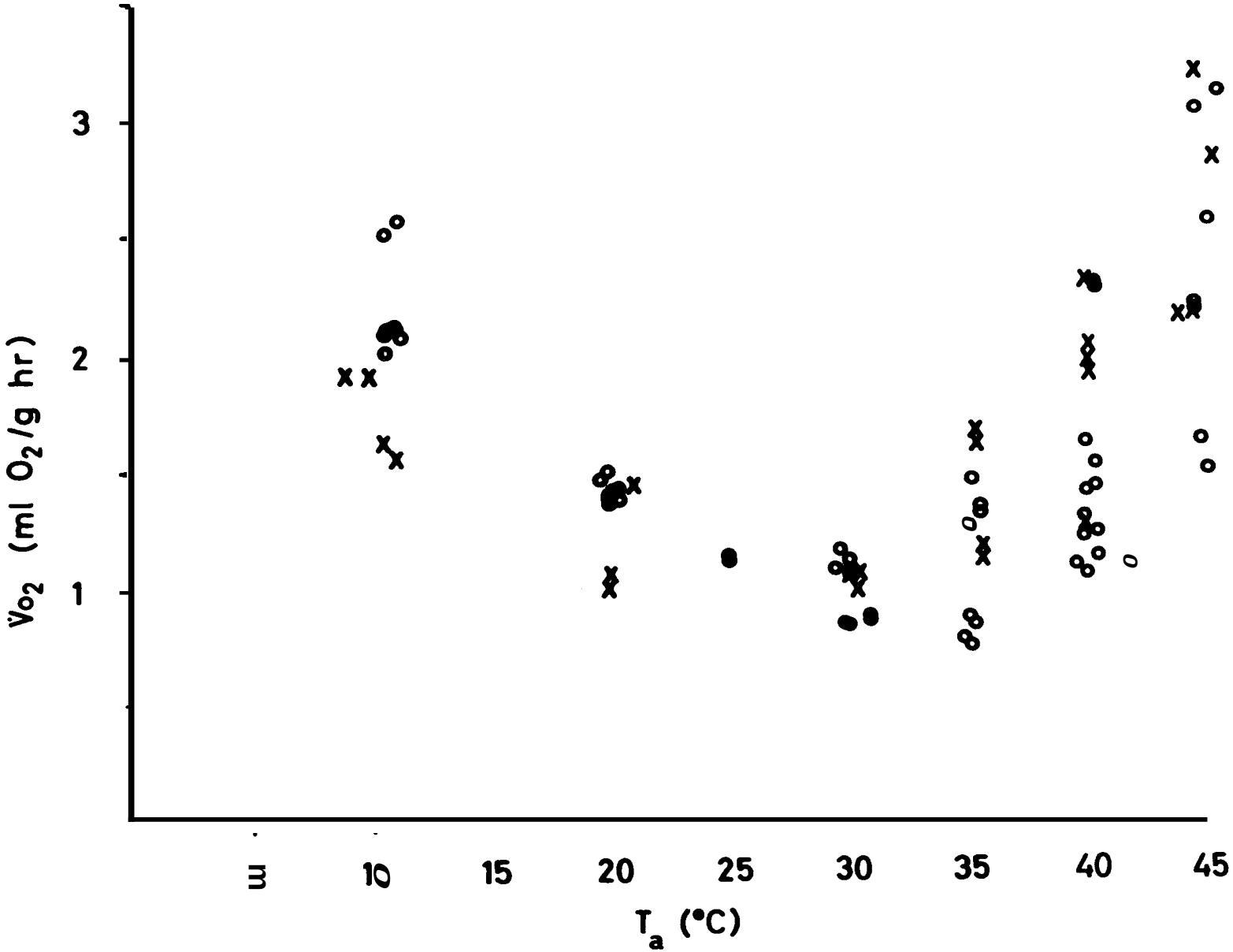

FIG. 2. The relationship between oxygen consumption ($\dot{V}_{O_2}$) and T_a in adult (0) and fledgling (X) Sooty Terns.

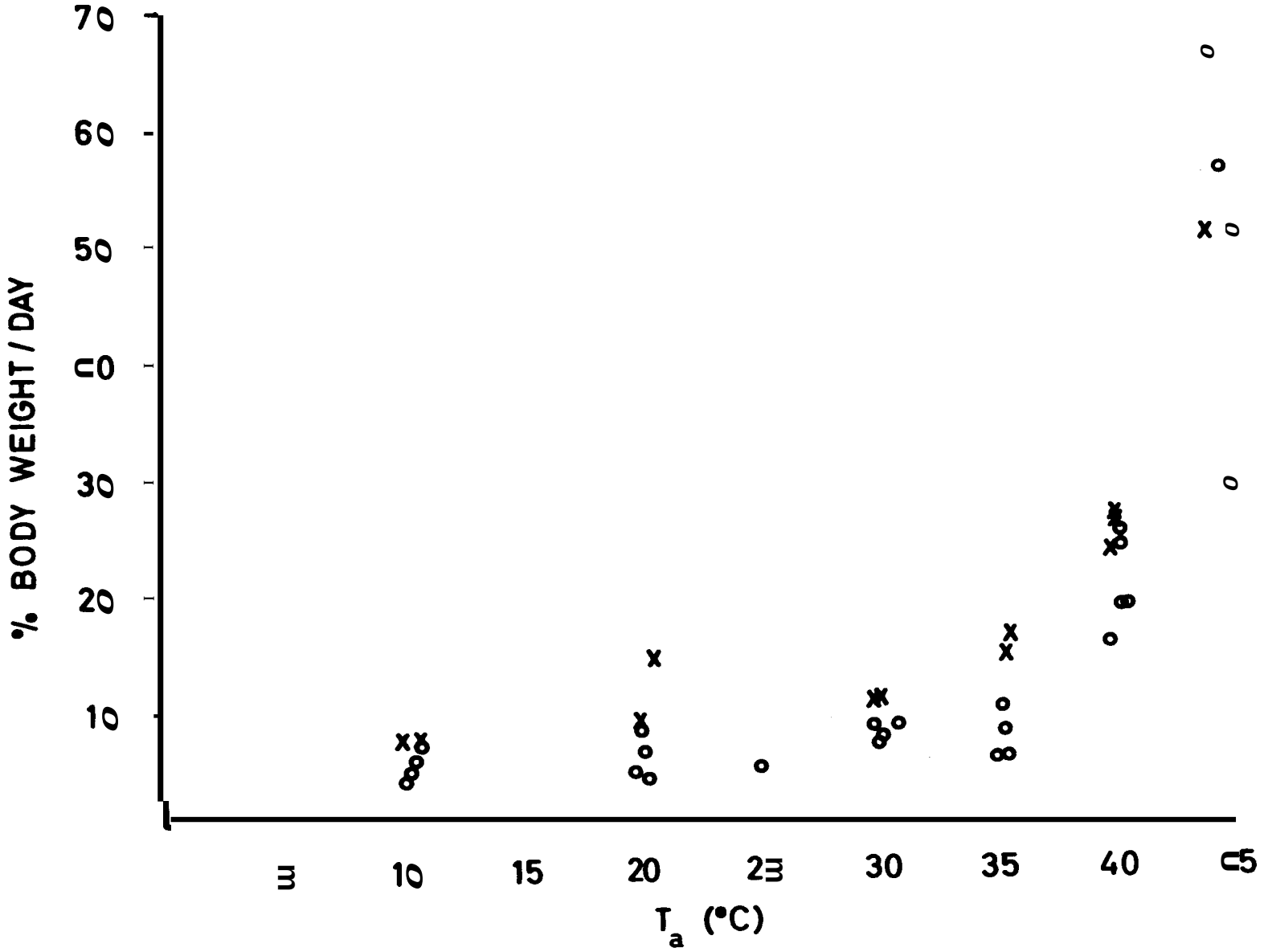

FIG. 3. Percentage of body weight lost by evaporation as a function of T_a in adult (0) and fledgling (X) Sooty Terns.

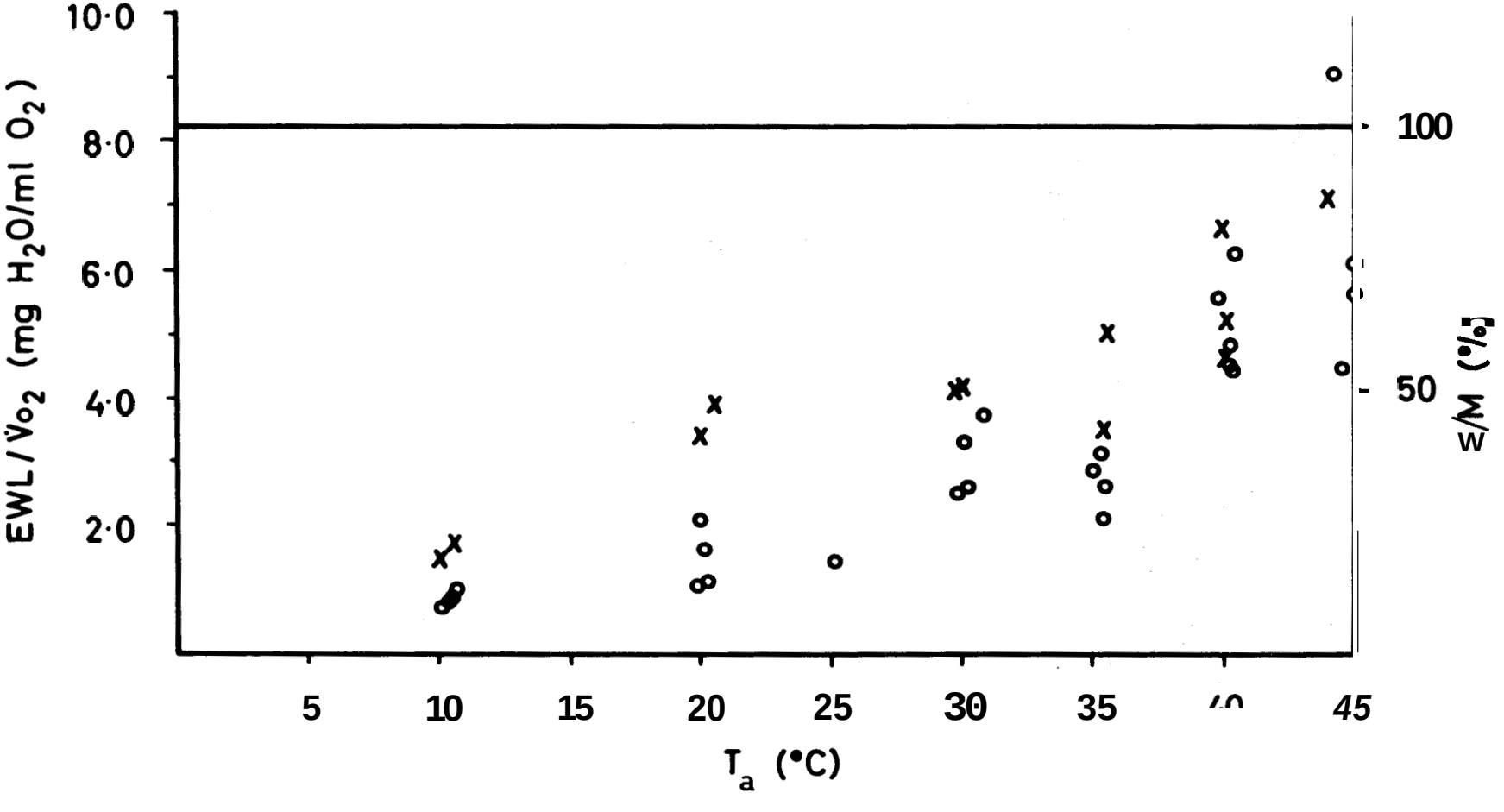

FIG. 4. The relationship between evaporative water loss (EWL), oxygen uptake ($\dot{V}_{O2}$), heat production (M) and T_a in adult (0) and fledgling (X) Sooty Terns. The left-hand ordinate expresses the ratios between evaporative water loss (EWL) and oxygen consumption ($\dot{V}_{O_2}$), while the right-hand ordinate expresses the ratios between evaporative heat dissipation (E) and metabolic heat production (M). The horizontal line indicates equality between E and M.

thermal conductances for adult and fledgling Sooty Terns are indicated in Fig. 5; the values are very stable for both age groups within and below thermal neutrality. At T_a = 10 and 20°C, the C of fledglings is conspicuously lower than that of adults, which is consistent with the observation that fledglings have a higher T_b (Fig. 1) and lower oxygen consumption (Fig. 2) at those temperatures. Thus fledglings appear to be more economical, energetically, at the lower temperatures, by virtue of more effective insulative capacities (down or subcutaneous fat, or a combination of both). This increased efficiency could be particularly important when the fledglings are independent from the parents at night, yet they are not fully self-sufficient in feeding. Dry thermal conductance of both adults and fledglings increases markedly and similarly above thermal neutrality.

A great deal of attention has been paid to the relationship between standard metabolic rate (SMR) and body weight in birds, and it is now well established that this is an indirect relationship, and that passerine birds generally have higher standard metabolic rates than do nonpasserines of the same size (see Dawson and Hudson 1970, for recent review). Further, Dawson and Hudson (ibid.) suggest the likelihood that within nonpasserine birds ordinal differences in size-related metabolism will be found, such as has recently been demonstrated for columbiform birds (Dawson and Bennett 1973). Size-related standard metabolism in birds has been further elucidated by Aschoff and fohl (1970), who have shown that in both passerine and nonpasserines standard metabolism measured during the active phase of the 24 hr period is predictably higher than that measured during the inactive phase. Very little information is available on the standard metabolism of charadriiform birds so that a detailed analysis of their size-related metabolism is premature at this time. However, our data lend themselves to comparisons with other nonpasserine birds. The standard metabolic rate of six Sooty Terns (four adults, two fledglings) at T_a = 30 ± SD, 0.5°C, and weighing an average of 147.5 ± SD, 11.3 g was 0.98 ± SD 0.11, ml O_2/ghr. This is equivalent to a standard metabolism of 16.65 kcal/24 hr (assuming 1 ml O_2 = 4.8 cal). Using Aschoff and Pohl's (1970) equation ($M = 91.0 \cdot W^{0.729}$, where M is standard metabolism in kcal/day, and W is body weight in kg) relating body size to standard metabolism in nonpasserine birds measured during the normal period of activity (daytime for diurnally-active birds such as terns), the predicted M for birds the size of ours is 22.55 kcal/24 hr. Thus the standard metabolic rate of our Sooty Terns is 74 percent of that predicted for a nonpasserine species. This is a substantial reduction in metabolism, but it remains to be seen whether such reductions are common among the Charadriiformes.

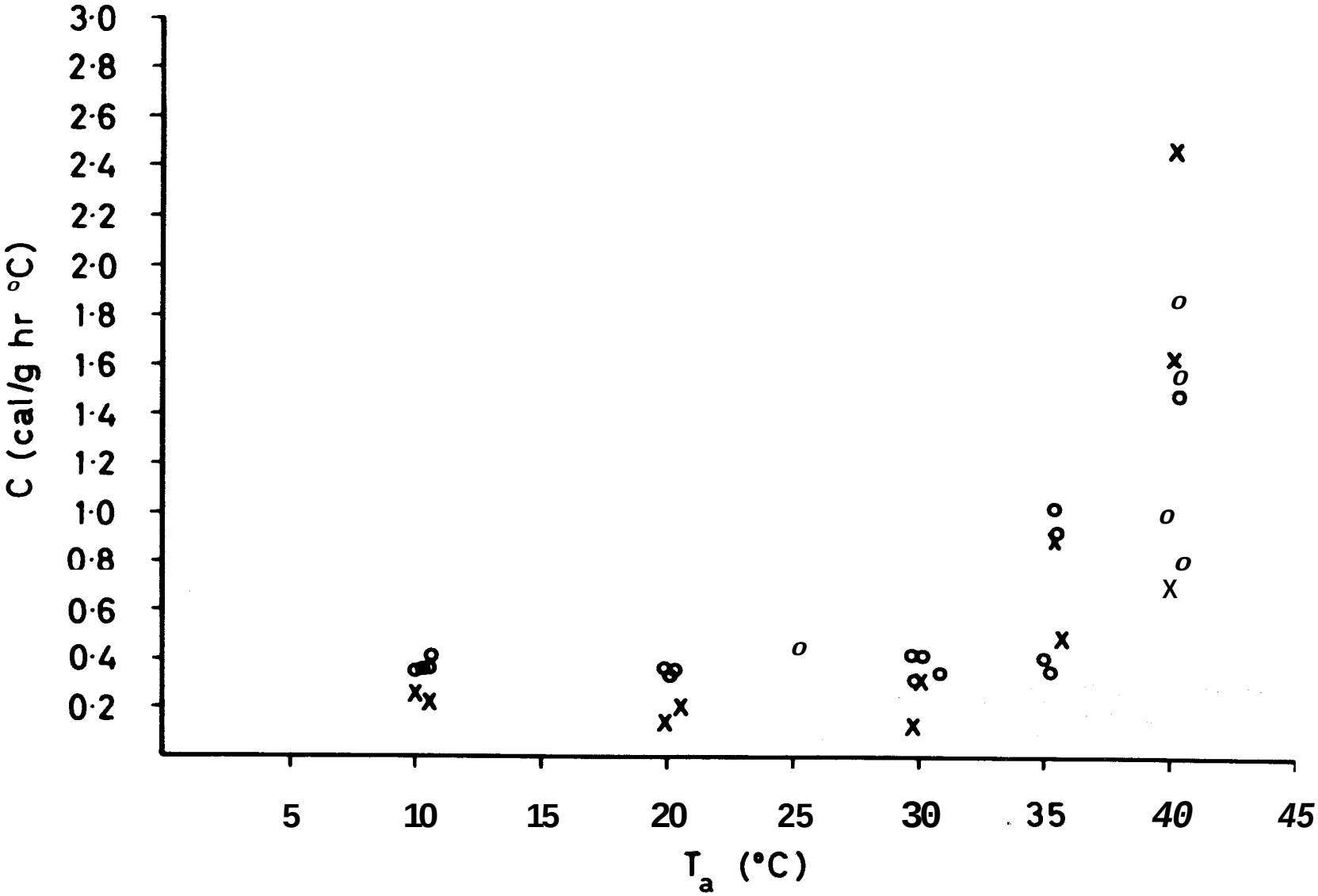

FIG. 5. **Dry** thermal conductance (C) as a function **of** T_a in adult (0) and fledgling (X) Sooty Terns. Calculated **from** the equation $C = (M-E)/(T_b-T_a)$. These calculations assume that 1.0 ml O_2 = *4.8* cal, and 1.0 **mg** H_2O = *0.58* cal.

A reduced metabolism and concomitant reduced rate of heat production in both adult and fledgling Sooty Terns is probably valuable in ameliorating the total heat load on these ground-nesting birds. This in fact may be the primary physiological adaptation of Sooty Terns to excessive heat, for they seem to have only modest capacities for evaporative cooling. Simultaneous measurements of T_b, T_a, oxygen consumption and EWL (Figs. 1 & 4) reveal certain discrepancies between measurements, in that four of seven birds tested at T_a = 44-45°C, had $T_b < T_a$ ($\bar{x}$, T_b of 44.3 vs. T_a of 44.6°C, respectively; Fig. 1), while only one out of five of these birds, for whom simultaneous measurements of metabolic heat production (M) and evaporative heat dissipation (E) were available, had M < E. Of these five birds one dissipated by evaporation 109.3 percent of the heat of metabolism at T_a = 44.2°C, while the other four dissipated, on the average, only 71 percent of M at a mean T_a of 44.7°C (see Table 2). The most likely explanation for this finding is that the four birds were storing heat and that their body temperature had not quite increased to that of the environment, within the relatively short experimental time period. Still another individual was removed prematurely from the experimental procedure when its body temperature reached 46°C to T_a = 44.7°C; this animal was dead on the following day, presumably due to excessive heat exposure. During exposure to T_a = 44 to 45°C, no gular flutter was apparent in any of the birds, but they all panted vigorously and were quite restless. Panting rates of six adult Sooty Terns at T_a = 44-45°C averaged 174 ± SD, 8.0 respirations/min, which is considerably less than the reported rates of gular flutter in other birds (Dawson and Hudson 1970).

Relative humidities (RH) and water vapor pressures in the respirometer chamber during heat exposure were calculated for each of the birds after the method of Lasiewski, et al. (1966). These, as indicated in Table 2, were extremely variable and the average was rather high ($\bar{x}$, RH = 51.4 ± SD, 16.5 percent, $\bar{x}$ WVP = 36.1 ± SD, 11.3 mm Hg). This average value though is at least 10 percent lower than the RH measured in the nesting colony (Table 1). It is possible that the humidities were sufficiently high to preclude effective evaporative cooling, but we doubt this since the single bird capable of dissipating more heat by evaporation than that produced by metabolism, was also subjected to the highest humidity (Table 2). Therefore, we must interpret the data to indicate that physiological mechanisms for the dissipation of heat by evaporation in the Sooty Tern are only moderately developed. This interpretation is consistent with the conclusion by Howell and Bartholomew (1962) regarding Sooty Tern chicks exposed to the sun on Midway Island, that ... "they are not able to dissipate by panting a quantity of heat greater than that

TABLE 2. Mean body temperatures (T_b), ambient temperatures (T_a), effectiveness of heat dissipation (E/M), and humidities in the respirometer chamber, for Sooty Terns at high temperatures.

Birds	T_a, °C	T_b, °C	$\frac{E}{M}$ x 100*	Humidity** RH, %	Humidity** WVP, mm Hg
adult	44.2	42.5	109.3	67.2	46.4
adult	45.0	43.4	73.1	24.8	17.8
adult	45.1	44.6	68.1	52.0	37.6
adult	44.6	45.3	53.5	62.9	44.3
fledgling	44.0	44.3	88.7	50.3	34.3

* E = total evaporative heat loss
M = heat production

** WVP = water vapor pressure
RH = relative humidity

produced by their own metabolism." Very likely this inefficiency in heat dissipation by the Sooty Tern is more related to the inability to control heat production while panting, than to the inability to mobilize water for evaporation. The Western Plumed Pigeon (Lophophaps ferruginea), a ground-dwelling Australian columbiform bird, uses energetically inexpensive gular flutter during exposure to heat, and at T_a = 44°C is able to dissipate, by evaporation, 140 percent of heat production (Dawson and Bennett 1973). Between at T_a of 35 and T_a of 45°C, the metabolic rate (heat production) increased only by a factor of about 1.1, while weight-relative water loss (heat dissipation) increases by a factor of about 5.0. In Sterna fuscata, under the same conditions of T_a (35 to 45°C), metabolism increases by a factor of 2.1, while weight-relative water loss increases by a factor of 5.0 (Figs. 2 & 3). Thus the lower heat production accompanying gular flutter in L. ferruginea most likely permits effective evaporative cooling.

It is doubtful though that Sooty Terns are often exposed to excessive heat loads, even in the direct sun on the nesting colonies. Howell and Bartholomew (1962) state that air temperatures on Midway Island rarely rise above 30°C, and that thermoregulation in adult Sooty Terns is accomplished without unusually heavy panting or special behavior patterns. Our data obtained on Manana Island (Table 1) show the T_b of adults and fledglings to be comparable to those exposed in the respirometer chambers to a T_a of 35 to 40°C. The air temperature (27-30.9°C) on Manana is within the thermal neutral zone determined in the laboratory. Thus we feel that a propitious choice of the nesting site, close to the moderating influence of the sea and exposed to sea breezes, is sufficient to enable adults and fledglings to cope with the moderate heat load imposed by the environment, without requiring specialized physiological mechanisms for heat dissipation. The combination of a depressed metabolism, a moderate capability for evaporative cooling and behavioral adjustments such as standing with head upwind and with wings slightly drooped, appear to be adequate.

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Key word index - Sooty Tern, Sterna fuscata, body temperature, oxygen consumption, evaporative heat loss, temperature regulation.

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